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Mesofauna in mixed liana or tree litter bags: Growth form does not matter, but location does

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ABSTRACT

Liana and tree leaves differ in several traits, with liana leaves generally exhibiting higher quality according to the leaf economic spectrum, which is also reflected in their litter. Differences in nutrient content and physical traits may influence the abundance and diversity of mesofauna inhabiting litter. This raises the question of whether liana and tree litter support different mesofauna communities during decomposition and what role lianas play in forest floor food webs.

We studied litter fauna from mixed litterbags containing liana, tree, or a mixture of both litters after 1, 3, 5, and 11 months of incubation in three tropical forest types in SW China. The litterbags contained representative species from each forest type. Fauna was initially identified to order level through morphological sorting per litterbag, then all fauna was pooled per forest type and incubation time and meta-barcoded.

We found no significant differences in fauna density or taxon richness between liana and tree litter, but observed differences across forest types. Fauna composition differed between forest types at most harvest times, with litter traits contributing marginally to the explained variation. Fauna taxon richness in each plot correlated positively with tree species richness, while fauna density showed a hump–shaped relationshipwith tree species. DNA barcoding data revealed similar patterns as morphological data but showed a trend of higher taxon richness in liana litter and compositional differences between liana and tree litter.

Overall, habitat types had a greater influence on the litter fauna than the short-term (1–11 months) litter mixtures provided in the litterbags.

1. Introduction

Lianas are an important growth form of tropical forests, with a growing number of studies in recent decades focusing on their ecological roles [1,2]. However, research exploring the role of lianas in food webs and their interactions with animals remains limited [3,4]. One such plant–animal interaction is litter decomposition, mediated by mesofauna (soil invertebrates of intermediate size, commonly defined as 0.1 mm - 2mm in length [5]). Decomposition involves a complex interplay of processes and various organisms, including fungi, bacteria, and invertebrates. Mesofauna can play a significant role in this process, and their contribution to biomass loss varies across ecosystems [6–9]. Mesofauna provide distinct ecological functions, they consume a high diversity of food sources [10], and can alter the microbe community by grazing as well as the environmental conditions in the topsoil [11]. Mesofauna communitiesare often used as bioindicator because certain taxonomic or functional groups aresensitive to environmental changes [12,13]. Litter decomposition studies, involving both lianas and trees, are scarce [14–17] and none of them have examined mesofauna from both ecological and taxonomic perspectives, by identifying or quantifying functional groups or invertebrate orders. Liana and tree leaves differ in several traits [18,19]; generally, liana leaves have higher quality than trees in terms of the leaf economic spectrum, and such difference is reflected in the traits of their litter, such as higher nitrogen content, lower leaf toughness, lower leaf dry matter content [17]. Variations in nutrient content and physical traits of litter may attract different mesofauna, consequently influencing the diversity and composition of mesofauna communities [20]. This raises the question of whether the differences in leaf litter derived from these two growth forms also shape the

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mesofauna communities involved in decomposition, potentially revealing the role of lianas in forest floor food webs.

Even though certain leaf traits of lianas and trees are different at larger scales [18], this is not necessarily hold true within local communities with a more limited set of plant species, where some overlaps would be found. The relative diversity and biomass of lianas can vary significantly depending on the forest type, and the differences (or similarities) in leaf traits between trees and lianas can also fluctuate based on the species composition of the communities. The underlying habitat differences in soil properties and climate, which influence plant community structure, will similarly affect mesofauna communities through linked aboveground–belowground interactions [21]. Accordingly, mesofauna effects on litter decomposition has been found to vary across habitat types at local and global scales [22,23]. Therefore, to better understand the relative importance of liana and tree leaf litter in mesofauna community assembly at a local scale, it is essential to consider multiple forest types.

Leaf litter serves not only as a food source but also as a habitat for diverse organisms, providing three-dimensional refugia [24] and creating diverse microclimates with varying water storage capacity [25]. Increasing litter diversity, quality, and functional richness enhances resource heterogeneity and niche availability, thereby promoting greater abundance and diversity of soil fauna across multiple trophic guilds, including decomposers and predators [26,27]. In this study, we examined the entire mesofauna community extracted from litterbags including all feeding guilds.

We tested how litter from dominant and/or common species of lianas and trees shelters different mesofauna communities across various tropical forest types within the same region of SW China [28–30]. A previous study using in the same forest plots and plant communities found that liana decomposed faster than tree litter and that both growth forms differed in several litter traits [17]. Our primary objective was to determine whether mesofauna communities in liana and tree litter mixtures differ in density, taxon richness, and composition over time. Additionally, we compared two identification methods: traditional morphological sorting under a microscope and DNA metabarcoding. We hypothesize that liana litter, being of higher quality than tree litter, supports a greater abundance and diversity of mesofauna, as well as a distinct mesofauna community composition compared to tree litter.

2. Material and methods

2.1. Study site

The study was carried out in the tropical forests surrounding the Xishuangbanna Tropical Botanical Garden, Menglun, Yunnan, China (21° 54' North, 101° 46' East, Fig. 1a). The region features hilly terrain with steep slopes, and altitudes ranging from 400 to 1400 m a.s.l. Annual precipitation averages 1500 mm, and the mean temperature is 21.8 °C. Xishuangbanna is home to more than 4000 species of angiosperms, and several distinct forest types are recognized in the region [31,32]. Our study encompasses three forest types [28,31]: A) a forest on rocky limestone with relatively low tree diversity from various families, referred to as "monsoon forest over limestone" (hereafter "limestone"); B) evergreen broad–leaved forest ("EBL"), dominated by Fagaceae family, mainly occurring on ridges; C) tropical seasonal rain forest ("TRF"), often located in valleys and lower elevations, with high tree species richness. Soil types in the area include laterite soil and lateritic red soil (EBL and TRF), and soil derived from limestone substrate of Permian origin (limestone) [33]. Soil variables can be found in data supplement S1. For each forest type, we selected five plots (Fig. 1b) of ca. 80 m^2. As a proxy for plant diversity, we used tree species richness estimated from larger survey plots that either encompassed or were adjacent to our litterbag experiment sites [28,30].

2.2. Species selection and litter collection

We aimed to select key liana and tree species or genera in each forest type. To this end, we examined the abundance, basal area, and Importance Value Index (IVI) of tree and liana species/genera in the region, ranking them based on their IVIs and their consistent importance across multiple data sources [28,31,34–37]. We then assessed the availability of litter for

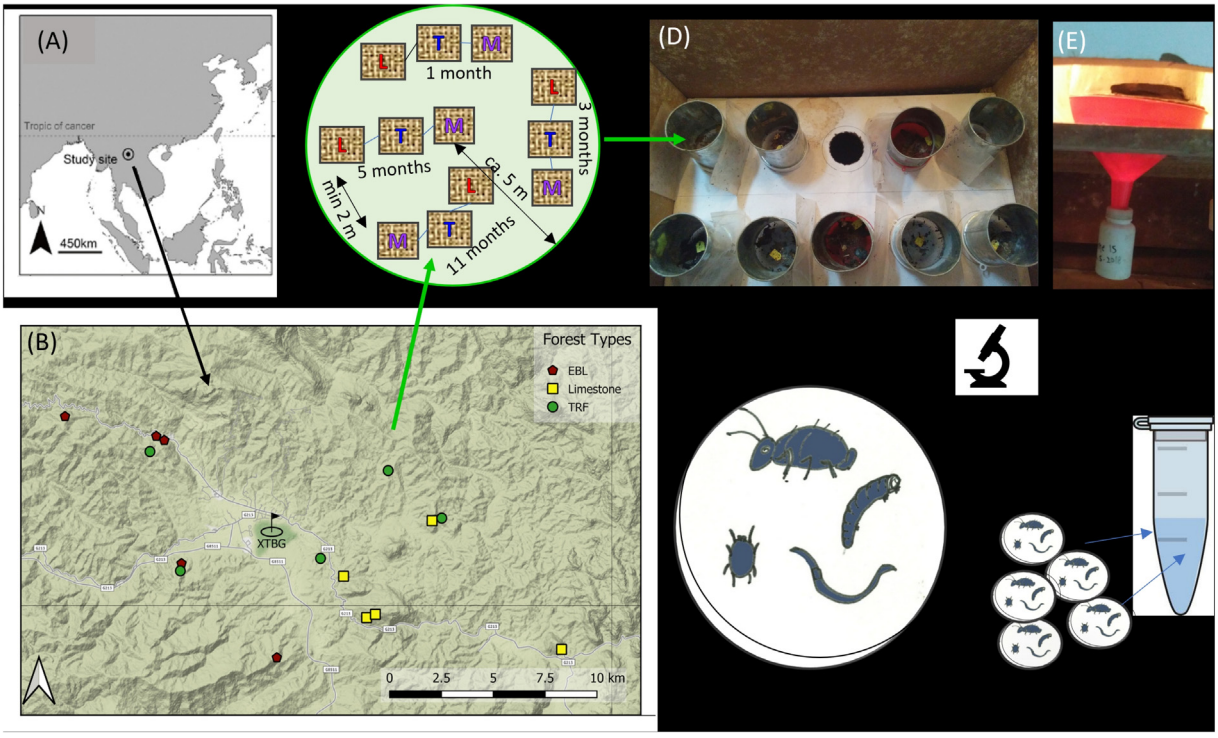

Fig. 1. A & B) Geographical location of the study plots around XTBG, Menglun, Xishuangbanna prefecture, Yunnan Province, China, C) bag set up in one plot with T = tree litter mixture, L = liana litter mixture, M = tree and liana litter mixture, D & E) mesofauna extraction in Berlese-Tullgren funnel (light bulbs on the lid), F) mesofauna of each bag was hand sorted (morphological data), afterwards pooled per forest type and barcoded.

each species from February to May 2017 and finalized a list of (morpho–) species for our experiment, with varying number of species across forest types which reflects the differences in species richness among them. In order to have similar species numbers in the mixtures in all three forest types, 28 species were used for the mixed coarse litterbags: 9 species in the TRF (5 tree and 4 liana species), 10 species in the EBL (5 tree, 5 liana) and 9 species in the limestone forest (5 tree, 4 liana), (see Table 1 for species names, family, growth form and habitat used in this study). Recently shed, not decomposed, clean, senescent leaf litter was collected from the ground in the garden and surrounding forests in February to May 2017. Litter was air dried the same day in the sun for 2–5 days and stored in air permeable bags.

2.3. Set up of field experiment

We filled 10 g of air–dried litter of liana species, tree species, or a combination of both into coarse mesh litterbags (2 mm mesh, 16 cm × 20 cm), ensuring an equal amount of litter from each species. Each litterbag was uniquely labelled, and litterbags of the same collection time were connected by a string and fixed with nails to the ground. Coarse litter was removed so that litterbags were placed directly on either the mineral soil or the soil organic layer, depending on the site conditions. At each plot, we deployed a total of 4 litterbag lines, with at least 2 m distance to the next within a circular area of approximately 5 m radius (Fig. 1c). The litterbags were installed in the field at the onset of the rainy season (late April to early May 2017). We carried out four collections at 1, 3, 5, and 11 months after the experiment began. In each of the three forest types, we used 5 plots (total 15 plots), in each plot we installed 12 litterbags (3 mixtures × 4 sampling times), resulting in 180 litterbags across the entire experiment and 5 replicates per treatment. Both litterbag placement and collectionswere completed within one week for each collection time. For each litterbag, post incubation biomass was determined by removing all soil and ingrown roots from the samples, and oven–drying at 65 °C until constant weight (weighed to 0.001 g accuracy). For more details, corrections of air–dry biomass to oven dry mass etc. see [17].

2.4. Litter traits and nutrients

Litter traits and nutrients were measured at the beginning of the experiment using the same litter material of each species used in the litterbag experiment. To measure specific leaf area and dry matter content, 10 leaves per species were moistened overnight in damp towels in the refrigerator. After blotting off excess water, the leaves were weighed, scanned, oven–dried, and weighed again. Leaf area was measured using ImageJ software. Leaf toughness, both in moistened and dry leaves for each species, was determined using the puncture method, which measures the force required to penetrate the leaf (IMADA digital force gauge Model DS2–50 N). Since wet and dry litter toughness were highly correlated ($r^2 = 0.92$), we used dry litter toughness as the trait.

We also analysed the content of macro– and micronutrients [nitrogen (N), phosphorus (P), potassium (K), carbon (C), magnesium (Mg), calcium (Ca), sulfur (S)], along with soluble tannins and lignin, for each species. Details of the methods are provided in Supplement A. As the litterbags contained multiple species, we calculated the average trait value, variance, and dissimilarity for each litterbag mix for use in the data analysis.

2.5. Mesofauna extraction and identification

We extracted mesofauna from all mixed litterbags at each collection time using Berlese-Tullgren funnels (Fig. 1d). Litterbags were removed from the forest floor, stored individually in plastic bags in the field, and transported to the laboratory, where we carefully placed the litter from each bag onto a 2 mm metal grid within the funnel. Samples were heated to ca. 35 °C with incandescent light bulbs for 48 h, causing the mesofauna to fall through the funnel into a collecting container filled with 95% alcohol. After mesofauna extraction, all soil and ingrown roots were carefully washed from the litter samples, which were then oven–dried until reaching a constant weight (measured to an accuracy of 0.001 g).

We sorted and counted mesofauna using a stereo microscope (Nikon SMZ745, max. 100× magnification) to a maximum taxonomic level of order for each sample (hereafter referred to as “invertebrate taxa” and

Table 1
Species, family, growth from (T = trees, L = lianas), and forest type used in the decomposition study. Average decomposition rate (k) over 4 harvest times x 5 replicates are listed for each species.

Species	Family	Growth form	Forest type	Average k coarse mesh ($month^{-1}$)	Average k fine mesh ($month^{-1}$)
Castanopsis echinocarpa Miq.	Fagaceae	T	EBL	0.175	0.103
Castanopsis fleuryi Hickel & A.Camus	Fagaceae	T	EBL	0.219	0.125
Castanopsis mekongensis A.Camus	Fagaceae	T	EBL	0.320	0.094
Celastrus “2“	Celastraceae	L	EBL	0.473	0.211
Celastrus paniculatus Willd.	Celastraceae	L	EBL	0.667	0.191
Craspedolobium unijugum (Gagnep.) Z. Wei & Pedley	Fabaceae	L	EBL	0.385	0.104
Cratoxylum cochinchinense (Lour.) Blume	Hypericaceae	T	EBL	0.354	0.077
Schima wallichii Choisy	Theaceae	T	EBL	0.248	0.108
Smilax hypoglauca Benth.	Smilacaceae	L	EBL	0.255	0.112
Spatholobus pulcher Dunn	Fabaceae	L	EBL	0.179	0.081
Bauhinia aurea H.Lev.	Fabaceae	L	limestone	0.300	0.099
Celtis philippensis Blanco	Cannabaceae	T	limestone	0.264	0.157
Cleistanthus sumatranus (Miq.) Müll.Arg	Phyllanthaceae	T	limestone	0.164	0.103
Gmelina arborea Roxb.	Lamiaceae	T	limestone	0.726	0.181
Lasiococca comberi Haines	Euphorbiaceae	T	limestone	0.190	0.123
Pristimera arborea (Roxb.) A.C. Sm.	Celastraceae	L	limestone	0.837	0.394
Combretum griffithii Van Heurck & Müll.Arg.	Combretaceae	L	limestone	0.414	0.250
Tetrameles nudiflorum R. Br.	Tetramelaceae	T	limestone	0.238	0.181
Tetrastigma “lime“	Vitaceae	L	limestone	0.259	0.093
Baccaurea ramiflora Lour.	Phyllanthaceae	T	TRF	0.236	0.094
Barringtonia macrostachya (Jack) Kurz	Lecythidaceae	T	TRF	0.348	0.201
Byttneria aspera Collebr. ex Wall. (before *B. grandifolia*)	Malvaceae	L	TRF	0.418	0.126
Combretum latifolium Blume	Combretaceae	L	TRF	0.480	0.244
Gnetum montanum Markgr.	Gnetaceae	L	TRF	0.432	0.127
Millettia leptobotrya Dunn	Fabaceae	T	TRF	0.164	0.132
Millettia pachycarpa Benth.	Fabaceae	L	TRF	0.265	0.141
Pometia tomentosa (now: Allophylus cobbe (L.) Raeusch.)	Sapindaceae	T	TRF	0.209	0.104
Terminalia myriocarpa Van Heurck & Müll. Arg.	Combretaceae	T	TRF	0.566	0.205

"morphological data") by literature keys [38–40] and group internal expert training. Hymenoptera was split into two groups: "ants" and "others". Due to logistical reasons, we pooled the five replicates (same mixture and same collection time from five plots) for metabarcoding, resulting in one sample per forest type, per litter mixture, and per collection time. These were initially 36 pooled samples, but 5 were lost during extraction process, leaving 31 samples for metabarcoding (hereafter referred to as "metabarcoding data").

2.6. DNA extraction and metabarcoding

We used a Power Soil DNA Isolation Kit (MoBio Laboratories Inc.) for DNA extraction, following the supplier's instructions. The primer set SSU_F04 (5'-GCTTGTCTCAAAGATTAAGCC-3′) and SSU_R22 (5'-GCCTGC TGCCTTCCTTGGA-3′) was used for targeting 18S rRNA 450 bp gene region [41]. PCRs followed the DAMe metabarcoding protocol [42,43], which performed three independent PCR replicates per sample, using twin tagged primers (F1-R1, F2-R2, …) in a final volume of 20 μl per triplicated sample, using 0.6 U Ex Taq HS DNA polymerase, 1 × Ex Taq Buffer (Mg^{2+} plus), 0.2 mM dNTP Mixture (TaKaRa, Biotechnology Co. Ltd., Dalian, China), 0.4 μM of each primer, 1 μl DMSO, 0.1 μg/μl BSA (Bovine Serum Albumin Solution, TaKaRa Biotechnology Co. Ltd., Dalian, China), and 2 μl genomic DNA. PCR amplification conditions were: initial denaturation at 98 °C for 5 min, followed by 27 cycles with 40 s at 98 °C, 30 s at 50 °C, 30 s at 72 °C, and a final extension of 10 min at 72 °C. PCR products were visualized on 2% agarose gels and mixed into 3 independent pools, purifying with beads (Agencourt AMPure XP kit, Beckman Coulter, Inc., USA), and then library building with the NEXTflex Rapid DNA-Seq Kit for Illumina (Bioo Scientific Corp., Austin, USA). The 3 libraries were sequenced on the Illumina MiSeq platform (300PE) at the Genomic Biodiversity Center, Kunming Institute of Zoology.

Raw MiSeq data were first trimmed for the presence of Illumina adapter sequences using AdapterRemoval 2.2.0 [44], and trimmed low–quality ends using sickle 1.33 [45]. We then denoised reads using the *Bayes Hammer* module in SPAdes 3.10.1 [46], and merged read pairs using PandaSeq 2.11 [47]. Sequences were demultiplexed to sample and filtered for tag–jumps using a modified version of DAMe that ignores heterogeneity spacers in the primers (github.com/shyamsg/DAMe, accessed 10 October 2020). We then only kept sequences that appeared in at least 2 of the 3 PCRs per sample, at a minimum 4 reads. We further filtered by removing sequences ≤400 bp length and using the de.

novo chimera search function in vsearch 2.4.3 [48]. Sequences were then clustered into 97% similarity Operational Taxonomic Units (OTUs) using SUMACLUST 1.0.20 [49] to generate OTU table. We used the R package 'lulu' 0.1.0 [50] with default parameters to combine likely 'parent' and 'child' OTUs that had failed to cluster. Finally, OTUs were assigned taxonomies using the Protist Ribosomal Reference database (PR^2, http://ssu-rrna.org/, [51]). We rechecked for new hits for each OTU on the order level in Genbank Nov 2023 and updated the order ID for OTUs.

2.7. Statistical analysis

2.7.1. Morphological data- influence of growth form, forest type, litter traits

For the morphological data (n = 180), we used log–transformed fauna abundance (individual counts per litterbag) and taxon richness as response variables. Predictors included forest type, litter mixture, incubation time, their interaction terms, and post–incubation litter biomass as fixed effects, with survey plot as a random effect in linear mixed–effects regression models (LMER). We conducted stepwise simplification of models based on likelihood ratio tests (LRT) and reported the results of the best models. The best models were selected using the following steps. We first tested if the random effect could be omitted, then sequentially removed interactions while retaining all main predictors (time, litter mixture, forest type), as all were of interest.

We applied a multivariate GLM (function *manyglm,* R package *mvabund* [52]) to test for compositional differences across groups (forest type, litter mix). The function fits a separate GLM to each taxon (taxa matrix ~ forest type * litter mix * month + biomass). The species matrix was presence–absence data, hence the error distribution for the GLM was binomialand we used LRT for stepwise simplification of the model. We used one NMDS (Bray–Curtis distance) per month for visualization. To assess whether the treatments influenced the taxa turnover in litter fauna, we calculated the beta–diversity of five mesofauna samples with identical litter mix collected at the same time (e.g., beta diversity of liana litterbag in five different plots of EBL forest at one month incubation) using the function *betadiver* from the R package *vegan* [53]. This resulted in 36 beta diversity values, which were tested in an additive GLM with forest type, time and litter mix as predictors and gaussian error distribution.

We also examined whether mesofauna density and taxon richness (litter mix pooled within one plot over time, 45 samples = 3 litter mix *15 plots) were related to plant diversity, using tree species richness per plot as a predictor. In case of fauna abundance, a quadratic function provided the best fit, while a linear model with log–transformed data was be used for taxon richness. Model fits were compared visually by diagnostic plots and explained variance.

We tested litter traits for autocorrelation across all plant species and retained nine traits that were potentially important for decomposition and/or showed variation between litter mixtures or forest types for further analysis (C to N ratio, P, K, Mg, Ca, Leaf Dry Matter Content, Specific Leaf Area, leaf area, and lignin). As each litterbag treatment contained several plant species, we calculated litter trait diversity (dissimilarity) by summing the Euclidean distances of traits between species in each litterbag treatment, divided by the number of species (*vegdist* function, R package *vegan*). We also used the average and variance of trait values for each litterbag treatment. The influence of traits on fauna abundance and taxon richness was tested using separate LMERs, following the full model described above, but without litter mix and by adding trait (count ~ month*forest type + biomass + trait). We compared the R^2 values of these models with trait against the full base model without trait to test the significance of trait effects.

2.7.2. DNA metabarcoding data– Influence of growth form, forest type, litter traits

For metabarcoding data, we analysed 31 samples, 36 pooled samples minus 5 samples lost during extraction. Taxonomic resolution was based on OTUs, and all analyses were conducted using the presence–absence matrix. Analyses were consistent with that used for the morphological data, but with OTUs as response variables. Due to the limited sample size and lack of spatial replicates, we did not include interaction terms of the predictors or treat plot as random effect. We, therefore, used an additive model without further simplification, using a GLM with a Poisson distribution, which provided the best fit. As with the morphological dataset, we applied multivariate GLM models (only additive) to test for compositional changes between groups, and used NMDs for visualization of compositional changes.

Since the replicate samples were pooled before DNA extraction, we did not calculate beta–diversity for each litter mixture. Additionally, no data analysis was conducted to examine the relationships between OTU richness and litter traits. Instead, we assessed the relationships between OTUs richness in each litter mixture type and the average tree species richness across forest types.

2.7.3. Comparisons of morphological vs. metabarcoding approaches

We compared the compatibility of the two methodological approaches (morphological sorting versus metabarcoding). To ensure consistency, we pooled the morphological data from the 5 spatial replicate samples, mirroring the treatment of the metabarcoding data, and excluded the exact samples missing from the metabarcoding dataset. This resulted in 31 samples for both methods. For the metabarcoding data, we used invertebrate order as the taxonomic resolution, matching the highest resolution in the morphological data. We excluded all unidentified taxa, expect for total abundance counts per sample (where no identification was involved).

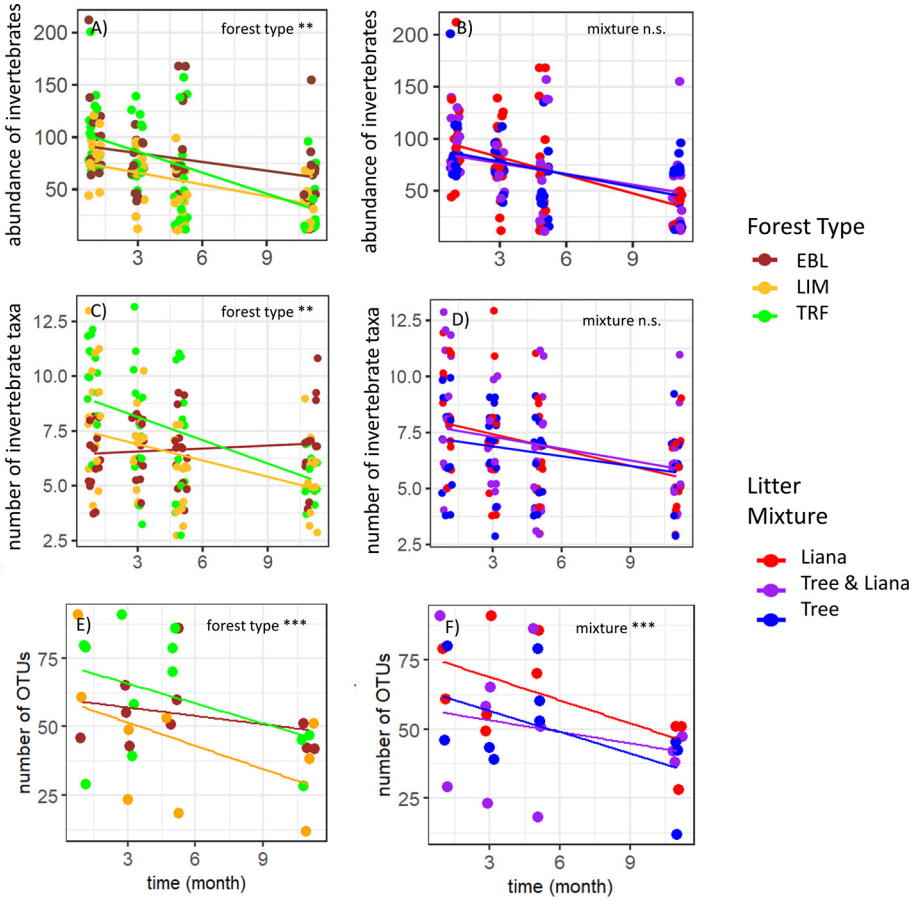

Fig. 2. Number of mesofaunal invertebrate individuals and taxa found per litter bag (180 bags). Litter bags had litter mixtures of lianas, trees, and both (lianas and trees) for three forest types (EBL = evergreen broad leaf forest, LIM = limestone forest, TRF = tropical rain forest), sampled after 1,3,5, and 11 months. Only significances concerning forest type and litter mixtures are indicated in the figure, for results of all variables and interactions in the model see Table S2 & S3.

Hymenoptera was divided into two groups; ants and other Hymenoptera. We then tested whether the individual counts (or sequence reads) per sample, the individual counts (or sequence reads) per order, and the number of orders per sample were correlated between the two methods. Non–metric multidimensional scaling (NMDS) with Bray–Curtis distance was conducted on both abundance and presence–absence data, and we compared the ordination of morphological and metabarcoding data with a procrustes analysis, using the function *protest* (R package *vegan*). Procrustes analysis compares ordination configurations after rotation and scaling, with significance assessed by permutation tests (999 permutations). We used NMDS to visualize the composition of a joint matrix of metabarcoding and morphological data, and the shifts in composition between the two methods were denoted by arrows.

3. Results

3.1. Influence of litter mixture and forest type on litter fauna - morphological data

Mesofauna abundance, taxon richness and litter biomass were all positively correlated. The correlation was the strongest between mesofauna abundance and litter biomass (log data, $R^2 = 0.634$, $p < 0.001$, Fig. S1), followed by taxon richness and abundance (log data, $R^2 = 0.528$, $p < 0.001$), and taxon richness and litter biomass (log data, $R^2 = 0.456$, $p < 0.001$).

Mesofauna abundance was significantly influenced by forest type ($F = 60.05$, $p = 0.003$), the interaction between forest type and month ($F = 5.14$, $p = 0.007$) and post–incubation litter biomass ($F = 22.58$, $p < 0.001$) (Table Supplement B.2). Over time, mesofauna abundance remained consistently greater in EBL than in limestone forest (Fig. 2a). At the onset of litter decomposition (1 month), TRF exhibited higher abundance than both EBL and limestone forest; however, its abundance declined more rapidly than EBL and limestone forests, becoming lower than in these two forest types (Fig. 2a). Litter mixtures of tree, liana, or both had no significant influence on mesofauna abundance (Fig. 2b, Table Supplement B.2).

Likewise, mesofauna taxon richness was significantly influenced by post-incubation litter biomass ($F = 24.73$, $p < 0.001$), forest type ($F = 4.99$, $p = 0.007$) and the interaction between forest type and month ($F = 7.76$, $p < 0.001$) (Table Supplement B.3). Overall, mesofauna taxon richness was lower in EBL forest than in TRF (Fig. 2c). In the early stages of litter decomposition (1 and 3 months), both TRF and limestone forest exhibited higher taxon richness than EBL; however, their taxon richness declined more rapidly than EBL, becoming lower than in EBL at 11 month (Fig. 2c). Litter mixtures had no significant influence on mesofauna taxon richness (Fig. 2d, Table Supplement B.3).

The multiple GLM results suggested that mesofauna community composition varied significantly with forest type (deviance = 150.62, Pr = 0.001), litter biomass (deviance = 76.84, pr = 0.001), and time (deviance = 196.11, pr = 0.001), but not with litter mixture (deviance = 81.31, pr = 0.085) (Supplement B.4, Fig. 3). Taxa that changed overtime were Iospoda, Isoptera and Opiliones, which were more important at early collection times as well as Aranae, Protura, Diplopoda, ants and Pseudoscorpions, which were mor important at late collection times. Beta diversity was higher in TRF than in EBL forest type, but no significant difference between liana and tree litter was found. (Supplement B.5 and B.6).

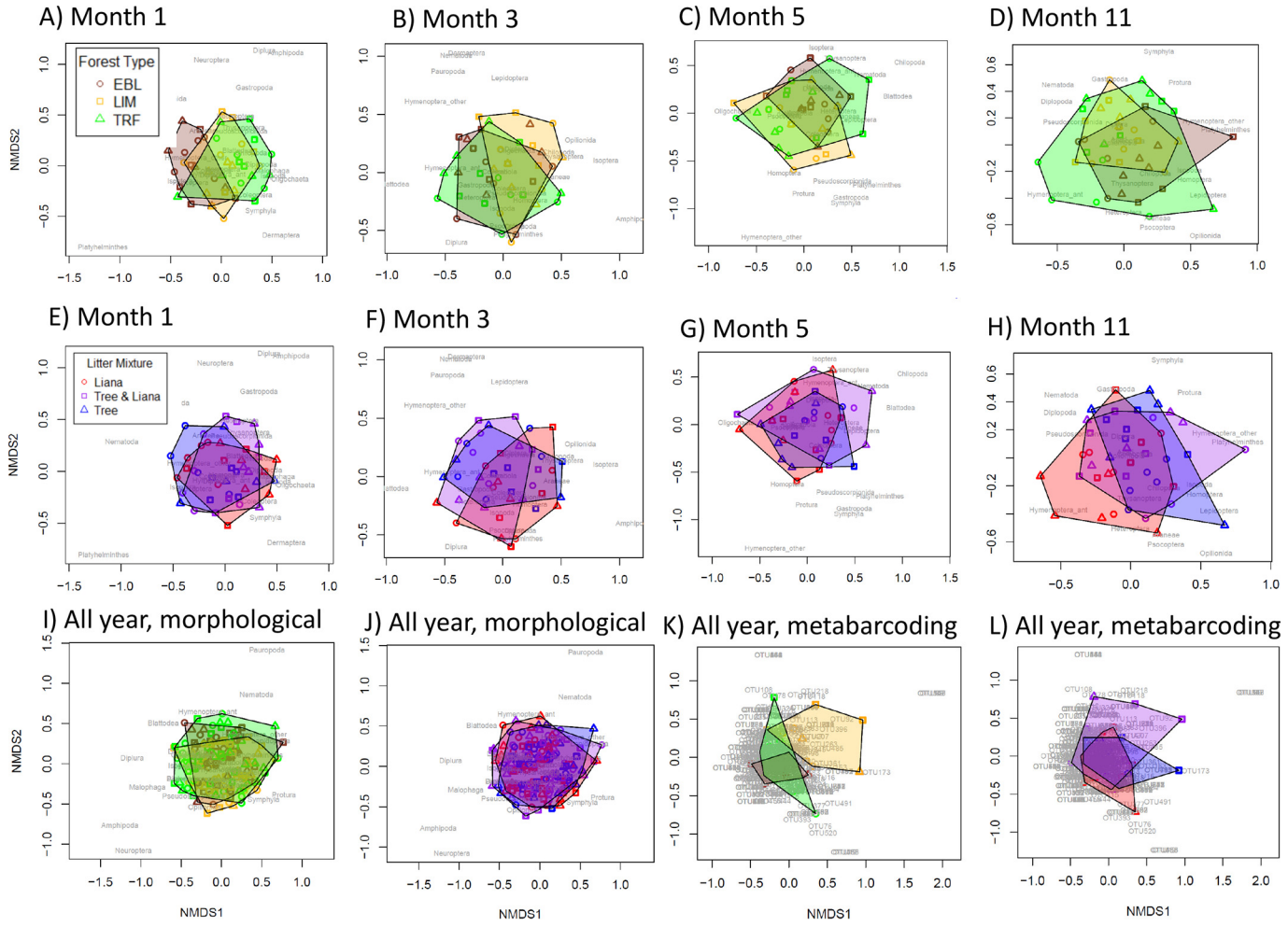

Fig. 3. Non-metric multidimensional scaling (NMDS) for presence/absence matrix for litter fauna: A-D) morphological data visualized per forest type after 1, 3, 5, 11 months, E-H) morphological data per litter mixture (liana, tree or both) after 1, 3, 5, 11 months, I-J): morphological data (four time periods pooled), K-L): operational taxonomic units (OTU) data from metabarcoding (four time periods pooled). Stress values are indicated in the right corner. Visualization only, for statistical analysis refer to "multivariate GLM".

None of litter traits added any explanatory power to the full models, contributing less than 1% to the R^2 of each model (Supplement Table B.7).

Fauna abundance showed a humped–shaped relationship with tree species richness, with a maximum abundance in plots with 30–40 tree species (Fig. 4a). Order richness increased with tree species richness (Fig. 4b, Supplement B.8). The pattern was consistent when fauna abundance and order richness per litterbag were divided by litter biomass.

3.2. Influence of litter mixture and forest type on litter fauna – Metabarcoding data

The data obtained by metabarcoding revealed that OTU richness was significantly influenced by forest type (Chisq = 245, $p = 0.005$), litter mixture (Chisq = 185, $p = 0.009$), and time (Chisq = 125, $p < 0.001$), but not litter biomass (Chisq <0.001, $p = 0.987$) (Supplement Table B.9). Over

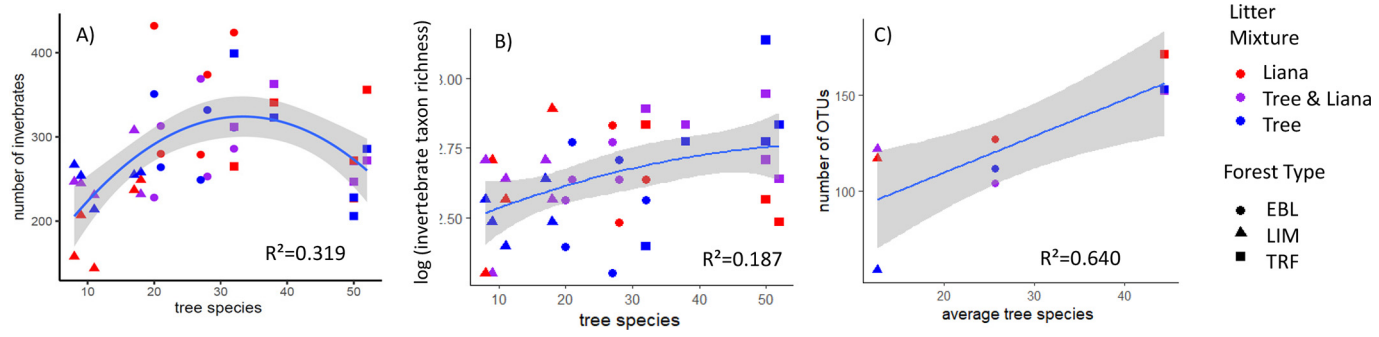

Fig. 4. Influence of tree species richness on mesofauna abundance and taxon richness: A) and B) are summed values for mesofauna per plot for each litter mix over all collection times versus the number of tree species per plot, C) summed operational taxonomic units (OTUs) of mesofauna per forest type for each litter mix over all collection times versus average tree species number of each forest type. Grey bands indicate 95% confidence intervals.

time, OTU richness remained consistently greater in TRF than in limestone forest (Fig. 2e). In the early stages of litter decomposition (1, 3 and 6 months), TRF exhibited higher OTU richness than EBL; however, its OTU richness declined more rapidly than EBL, becoming lower than in EBL at 11 month (Fig. 2e). Over time, OTU richness in liana litterbags remained greater than in the other litter mixtures (tree only litter or liana–tree mixture litter) (Fig. 2f, Supplement Table B.9).

The multiple GLM results suggested that OTU–based community composition varied significantly with forest type (deviance = 1516, p = 0.001), litter mixture (deviance = 1427, p = 0.005), and litter biomass (deviance = 951, p = 0.001), but not with time (deviance = 526, p = 0.264) (Fig. 3, Supplement B.12). OTU richness linearly increased with tree species richness (Fig. 4c, Supplement Table B.10).

3.3. Method comparison of morphological sorting vs. metabarcoding

Morphological data was represented by a total of 31 invertebrate taxa, and metabarcoding data was represented by 30 (Supplement Fig. B.11). Each method had similar numbers of taxa that were uniquely found per sample in either method (Fig. 5a). Most common taxa found additionally per sample by metabarcoding included Oligochaeta, Nematoda, Platyhelminthes, Lepidoptera, Copepoda, and Polychaeta and for the morphological data included Isoptera, Heteroptera, Hymenoptera (non–ants), Symphyla, Protura, and Gastropoda. Despite the presence of some unique taxa per sample collected by different methods, the taxon richness was well correlated between morphological identification and metabarcoding (Fig. 5b, Table 2). Other metrics, such as mesofauna abundance (and sequence reads, Supplement Fig. B.12) and community composition, were also significantly correlated between the two methods (Table 2).

Table 2
Relationships of mesofauna data obtained by morphological identification and metabarcoding. Two sets of data (morphological identification and metabarcoding) are comparable, as both data consisted of the same taxonomic resolution and the levels of experimental treatments. Results from Pearson's correlation for univariate data, and Procrustes correlation of NMDS for multivariate data with significance assessed by 999 permutations.

Pearson's correlation	R	p
Counts of individuals vs. sequence reads per sample	0.410	0.022*
Log (Counts of individuals) vs. log (sequence reads) per taxon	0.716	<0.001***
Number of taxa (invertebrate orders) per sample	0.610	<0.001***
Procrustes correlation		
NMDS abundance data	0.532	0.001**
NMDS presence absence data	0.511	0.001**

4. Discussion

Litter originated from lianas or trees did not influence most of our observed mesofauna patterns, and litter traits did not play a major role either; however, forest type consistently influenced litter mesofauna. As a result, we reject our hypothesis that fauna would differ between liana and tree litterbags. Despite liana litter mixture having on average slightly higher N and lower tannin content, LDMC, and toughness than tree litter mixtures, these differences may have been too small to translate into biologically meaningful effects for mesofauna. Litter chemistry and structure played a limited role compared with broader habitat conditions such as forest type. Another possibility is that synergistic or antagonistic interactions in litter mixtures decreased the influence of single litter traits [54], however in our case neither trait dissimilarity nor trait variance in litter mixtures had any effect on the mesofauna. In our study, mesofauna in tropical rain forest and limestone forest differed in several aspects. Forest type encompasses many factors such as microclimate, litter standing crop characteristics (e.g., litter amount and quality), tree species richness, composition and soil properties, which we could not all include in our models. In summary, limestone forest was characterized by higher soil pH, approximately twice the phosphorus and three times the calcium concentrations, higher organic matter content, and a greater silt fraction compared with tropical rain forest. In contrast, tropical rain forest harboured roughly three times higher tree species richness and had a greater sand fraction. Limestone forest may also experience stronger water limitation due to its shallow soils and porous karst bedrock [55,56].Our study suggests that long–term habitat structure, rather than short–term litter contributions in the litterbags, was the primary driver of these patterns. The following section provides a detailed interpretation of individual aspects.

4.1. Biomass

Not surprisingly, greater litter mass supported higher mesofauna density and taxon richness, litterfall was found positively related to fauna diversity and abundance e.g. in studies in Andean cloud forest [57]. While this may seem obvious, more litter mass provides not only more food by the increase of the soil organic horizon but also more diverse and complex microhabitats with diverse physical traits and 3–D structures [58]. Physical microhabitats within litter can be a major determinant for litter fauna [59], and as such again indirectly influence processes where the litter fauna is involved like decomposition [60]. As the mesofauna communities of our study consisted of multiple trophic levels, including predators such as spiders or predatory bugs, the presence of pockets and other structures for hiding becomes crucial. This may dilute the effect of chemical litter traits, especially for fauna not directly consuming litter or biofilms on litter surfaces. Tough, slow–decaying litter can, therefore, support more mesofauna, with additional food sources potentially originating from soil particles, in–growing roots, fungi, and other organic matter. However, dividing the community into feeding guilds proved difficult at the morphological order level, as many orders contain various feeding guilds and identification from metabarcoding data can be unreliable. Restricting the

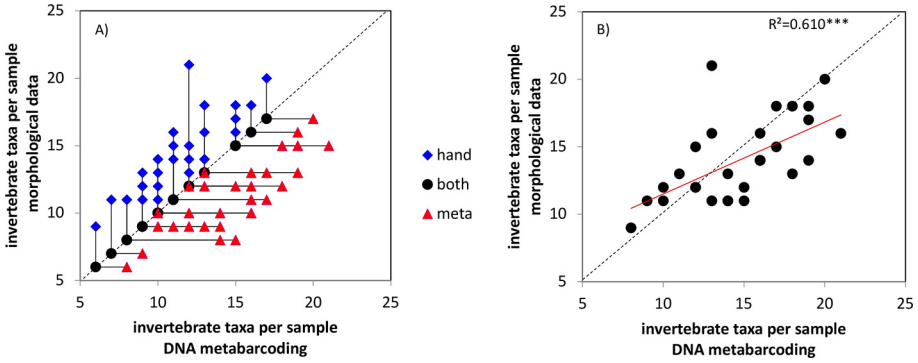

Fig. 5. A) Number of invertebrate taxa of the same identity found in both methods (black), and additional taxa only found by one of the methods (blue - morphological data, pink - metabarcoding), B) number of invertebrate taxa per sample found with two different methods, disregarding the identity of the taxa. Dash line represents the 1:1 line, red line represents the correlation.

analysis to strict decomposer guilds, such as diplopods, would reduce our dataset to a size too small for meaningful analysis.

At the early stages of decomposition, when the litter biomass was still abundant and relatively similar across the litterbags, litter quality might have stronger influence than in later stages, when litter quality becomes functionally similar [61]. However, in our case, forest type was significant at the beginning of the decay process, while litter mixture was not, indicating a strong location effect rather than litter quality effect. This was also supported by the fact that litter traits did not explain mesofauna patterns. In fact, the importance of the surrounding environmental matrix for decomposer activity is increasingly recognized, as both litter quality and matrix quality can alter the direction and strength of interactions between litter traits and local decomposer communities [62].

4.2. Tree species richness and mesofauna

We found mesofauna taxon richness were linked to tree species richness of the forest. Global surveys of soil fauna abundance found mid–latitude peaks for earthworms [63], and even further north for nematodes or collembola [64,65] resulting in a U–shaped curve across latitudes with the lowest values in the tropics (and deserts). This suggests that soil fauna abundance does not necessarily increase with plant diversity, which peaks globally at low latitudes. Locally restricted experiments in temperate grasslands generally show an increase in mesofauna density with plant diversity, though this varies over time and across faunal groups [66]. Soil fauna diversity also follows different patterns; for example, Collembola diversity peaks in the tropics, coinciding with plant diversity [65], while earthworms are most diverse at mid–latitudes [63]. A global study using DNA data across all phyla found that soil fauna diversity was actually lower in regions with high above–ground biodiversity [67]. Meta-analyses from temperate forests have generally reported positive effects of increasing plant species richness on soil fauna communities, and a broader comparisons of mixed plant communities versus monocultures similarly found higher soil fauna abundance and richness in systems with higher plant diversity [26,59]. These examples demonstrate that the relationship between above– and below–ground diversity depends heavily on the scale of the study, faunal groups, method and depth of identification (morphological identification versus metabarcoding) as well as on the fauna sampling method itself, e.g. if litterbags are used [68].

Our local dataset, while limited to a small scale in terms of available plant species, climate, and edaphic factors, showed an increase in mesofauna taxon richness with tree species richness, both for morphological and metabarcoding data. Assuming that our litterbags acted as baits for the majority of mesofauna in a given habitat, the long–term litter input from surrounding vegetation likely shaped the fauna communities in addition to climatic and edaphic factors. Greater tree species richness may increase niche diversification for litter fauna, as differences in litter resources—chemical, physical, or seasonal—are expected to increase with tree diversity [59].

The hump–shaped curve of mesofauna abundance versus tree species richness that we observed might reflect mechanisms beyond tree species richness. The soil fauna abundance peaked mainly at EBL plots, which had medium tree species richness, and was unexpectedly low in divers tropical rain forest. One possible explanation is variation in litter layer structure and persistence among forest types. EBL plots were characterized by tougher and more slowly decomposing litter, which may promote thicker and more stable litter layers that provide favourable microhabitats for mesofauna. From our observation, limestone forest (mainly low tree species richness) had shallow soils and sparse litter, and some tropical rainforest plots (mainly high tree species richness) in moist valleys appeared to have high litter turnover, also resulting in thin litter layers, which could decrease fauna abundance. Previous studies have shown that litter biomass and litterfall can positively influence soil fauna abundance [57,69]. Another explanation can be a facilitation effect in the begin of the curve (more tree species, more mesofauna) and a dilution effect at the end with higher tree species richness. This pattern was described regarding tree diversity and pest diversity [70].

4.3. Local pattern of mesofauna

A previous study examined mesofauna in two of the forest types we used (EBL and TRF) by employing 2 mm mesh litterbags filled with mixed litter and the same level of taxonomic identification [71]. The results showed no significant differences in mesofauna abundance or taxon richness between TRF and EBL, which aligns with our findings. In our study, limestone forest often showed distinct differences compared to the other two forest types, but differences between EBL and TRF were generally non–significant [72].

4.4. Limitations and future recommendations

We encountered two limitations in this study. First, due to financial constraints, we pooled samples within each forest type for metabarcoding, which resulted in a loss of spatial resolution. Consequently, we considered metabarcoding as supplementary data. Additionally, abundance data (number of reads) from metabarcoding can be skewed by PCR biases and requires taxon–specific corrections [73], we thus focused on qualitative data from metabarcoding. Morphological identification also had its challenges; for instance, worm–like organisms were sometimes taxonomically challenging to identify. However, as for any fauna group, established identification keys and expert assessment could have substantially improved taxonomic resolution. Despite these drawbacks, DNA barcoding trends largely aligned with the morphological data, and the correlations between the two methods were significant. The difference between forest types in mesofauna taxon richness was consistent with both methods. However, regarding litter mixes, the metabarcoding fulfilled our hypothesis of greater taxon richness and distinct community composition of mesofauna in liana litter compared to trees and tree–liana mixture, whereas morphological data did not. This difference can be attributed to higher beta diversity from the morphological data in liana litterbags that increased alpha diversity of the pooled samples used for metabarcoding. This undermined the ecological implications of metabarcoding data or /and higher level of morphological identification. Other studies comparing soil fauna communities based on morphological identification and metabarcoding often reported limited overlap in species identity and sometimes higher species richness in morphologically datasets. Such discrepancies likely arise from methodological differences, including primer bias, sequencing platforms, incomplete genetic reference databases, and differences in taxonomic resolution. However, both approaches typically recover similar ecological patterns, with community shifts and richness responses mirroring each other across treatments and environmental gradients [74–77].

Another limitation was the plant species richness within the litter mixtures. Our design did not allow us to test whether the inclusion of a particular plant species altered the mesofauna community, as we did not extract fauna from single–species litterbags. Additionally, litterbags containing only trees or only lianas had similar plant species numbers and litterbags with liana–tree combinations doubled as many plant species. However, despite this difference in species number, we found no significant increase in mesofauna abundance or taxon richness in the mixed liana–tree litterbags. For future studies, we recommend using single–species litterbags; although this may not fully replicate the natural conditions [78]. Single species litterbags would allow for more precise identification of species–specific effects on mesofauna communities. It would also be beneficial to include a standard litter type in all plots to assess location effects independently from local plant species.

5. Conclusion

In our setup, we did not observe consistent differences between mesofauna abundance, richness and composition in tree versus liana litter,

even so we included several forest types. In a natural setting, decomposing litter with different traits could attract and shape mesofauna communities. In our study, this was not the case; rather, we found that the location was likely the primary driver of the mesofauna community in this study. This emphasizes the importance of long–term environmental influences on the fauna, rather than our short–term litter provided in the litterbags.

CRediT authorship contribution statement

Mareike Roeder: Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization, Writing – original draft. **Xiaodong Yang:** Resources, Methodology, Writing – original draft. **Gbadamassi G.O. Dossa:** Investigation, Writing – original draft. **Masatoshi Katabuchi:** Formal analysis. **Chunyan Yang:** Methodology, Formal analysis, Writing – original draft. **Akihiro Nakamura:** Resources, Formal analysis, Writing – original draft.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecofro.2026.06.004.

Data availability

All data is provided in Supplement S1.

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